Numerical ordinality in a wild nectarivore

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Abstract

Ordinality is a numerical property that nectarivores may use to remember the specific order in which to visit a sequence of flowers, a foraging strategy also known as traplining. In this experiment, we tested whether wild, free-living rufous hummingbirds (*Selasphorus rufus*) could use ordinality to visit a rewarded flower. Birds were presented with a series of linear arrays of 10 artificial flowers; only one flower in each array was rewarded with sucrose solution. During training, birds learned to locate the correct flower independent of absolute spatial location. The birds' accuracy was independent of the rewarded ordinal position (1st, 2nd, 3rd or 4th), which suggests that they used an object-indexing mechanism of numerical processing, rather than a magnitude-based system. When distance cues between flowers were made irrelevant during test trials, birds could still locate the correct flower. The distribution of errors during both training and testing indicates that the birds may have used a so-called 'working up' strategy to locate the correct ordinal position. These results provide the first demonstration of numerical ordinal abilities in a wild vertebrate and suggest that such abilities could be used during foraging in the wild.

Introduction

Number is an emergent property of the world that defines quantities of individually discriminable sets of objects [1]. Number exists independent of sensory modality, and is considered more reliable than sensory-dependent stimuli [2]. The ability to comprehend number has the potential to profoundly influence an animal's fitness by affecting aspects of its life such as foraging, breeding, and conflict [3, 4]. However, the investigation of numerical cognition research has often been rather anthropocentric, with attempts to discover whether or not animals have human-like mathematical abilities, such as the ability to count [5]. This approach can then become entangled in definitional issues as to what constitutes 'counting', which distract from study of the ecological and evolutionary significance of numerical abilities. A different approach is to examine the numerical abilities of animals in relation to ecological 'problems' that animals solve on a daily basis [6]. Such an approach acknowledges that animals' numerical abilities may have been shaped by the ecological and evolutionary pressures of their natural environments.

Many human numerical abilities, such as advanced mathematics, are possible only as a result of our species' linguistic abilities, especially the ability to verbally label numbers [2]. However, research on languages without number words demonstrates that language is not a prerequisite to having a number sense, which suggests the existence of pre-verbal numerical cognitive mechanisms [7]. There appear to be two pre-verbal systems [8, 9]. One is an object-indexing system used to process small numerosities (numerical values): each item in a set is processed as a discrete unit, allowing an exact representation of numerosity. The upper limit of the object-indexing system is around four items in humans, but may be higher in some animals [10]. Larger numerosities are processed by an analogue magnitude system in which numerosities are represented as imprecise magnitudes. This second system abides by Weber's Law:

discrimination between numerosities is dependent on their relative magnitudes. The point at which animals switch between mechanisms appears to depend not only on absolute amount, but also on variables such as experience, attentional load, and the spatial characteristics of items in a set [8].

Cardinality is the property of number that describes the final value of a set. For instance, a set of three objects has a cardinality of three. Experimentally, cardinality is investigated primarily using numerosity discrimination tasks, which test whether animals can differentiate between cardinalities independent of the physical characteristics of the sets being compared. Numerosity discrimination is taxonomically widespread [e.g. 11, 12, 13,14]. Numerosity discrimination tasks do not, however, explicitly test for an understanding of the relationships between numbers. This requires an understanding of ordinality, a numerical property describing the sequential relationships between items in a set [15]. While an understanding of cardinality allows discrimination between the quantities '1', '2', and '3', ordinality allows one to understand that the 3rd item in a set comes after the 2nd, and that both come after the 1st.

An understanding of numerical ordinality would allow animals to exploit the inherent reliability of numerical aspects of their environment to their benefit. Studies on Alex, an African grey parrot (*Psittacus erithacus*), were among the first to show that animals possess ordinal mechanisms: Alex could spontaneously infer the cardinal value of a numerosity based on its ordinal position [16] while rats [17], guppies [18], monkeys [19], and bees [20] can all learn to re-locate spatially presented ordinalities with only minimal training. However, untrained success in laboratory paradigms does not indicate the contexts (if any) in which numerical ordinality is used by wild animals: animals in the lab may not necessarily use the same cognitive mechanisms

as those in the wild, even on similar tasks [21] and ordinality demonstrated in the laboratory can sometimes be achieved by subjects associating non-numerical cues with the order of items [22].

Hypothesising about ecological contexts in which animals may use numerical ordinality allows for the construction of testing paradigms that better reflect the pressures that wild animals are likely to face. One such context is during navigation between food patches whereby an animal may be able to return to a food patch based on the ordinal positions of landmarks. For example, Petrazzini et al., [18] suggested that guppies may use the ordinal position of landmarks as a guide to navigate within the rivers in which they live, where other cues are often unreliable. Furthermore, wild bees can use ordinality when visiting multiple nectaries on a single flower during foraging [4]. With the exception of this latter study, however, there has been little, if any, research into the ordinal abilities of wild, free-living animals in their natural habitats. Studying animals in the wild is advantageous, as it allows animals to solve problems without the stressors present in the lab.

Rufous hummingbirds (*Selasphorus rufus*) are a species that has been used as a model to investigate a variety of cognitive phenomena in the wild [23, 24]. Several aspects of their life history make them ideal wild subjects for cognitive experiments. Males of the species form individual territories in which they are easily observable, they can be marked for individual identification and trained to feed from artificial flowers, which they will re-visit every 10-15 minutes. Past research has shown that rufous hummingbirds forage primarily using spatial information [25] and can learn the re-fill rates of artificial flowers [26]. The knowledge of the spatial positions and re-fill rates of flowers within their territories could allow territorial males to form traplines between flowers in their territories. Traplining is a foraging strategy in which animals use only a fraction of the many possible routes that they could travel between a series of

food patches [27]. And, indeed, rufous hummingbirds will engage in traplining behaviour while visiting a sequence of rewarded locations [28, 29]. These birds might develop a trapline by using a memorised sequence of movements (i.e. associative chaining). But it is also possible that they use ordinal information to form traplines by assigning each artificial flower a numerical value and visiting them in order.

In order to test whether rufous hummingbirds could use ordinal information while foraging, we designed an experiment to test the birds' ability to re-locate a flower based only on its ordinal position in an array. Success by the birds would provide the first concrete evidence of ordinal numerical abilities in a wild vertebrate, assist with dispelling criticism about the ecological irrelevance of number, and provide a possible mechanism by which rufous hummingbirds can form traplines.

Methods

Subjects and Study Site

The subjects were nine wild male rufous hummingbirds observed in the Westcastle Valley, eastern Rocky Mountains, Alberta, Canada (N49.349153, W114.410864) between May and July 2017. Rufous hummingbirds winter in Mexico and begin to arrive in the valley in May. Prior to the birds' arrival, artificial feeders containing 20% sucrose solution were placed at sites throughout the valley, to encourage males to establish territories around them. After an initial period of observation to determine that a male had consolidated its territory around an artificial feeder, the territorial bird was trapped, marked with non-toxic ink for identification during experimentation, and released.

Initial Training

Each hummingbird was trained to feed from artificial flowers containing 25% sucrose solution. Artificial flowers consisted of a coloured foam disk, 6 cm in diameter, with a central 1.5 ml centrifuge tube. Each flower was affixed to a wooden stake, 60 cm long, which could be inserted vertically into the ground as in Figure 1 a/b. Once a bird had been trained to feed from the artificial flower in the experimental arena, the experimental training phase began.

Experimental Training

A male's feeder was removed during the hours of the experiment (returned at night and during intervals of precipitation). Birds were presented with a linear array of ten identical artificial flowers (F1-10), spaced at intervals of 20 cm from each other. One end of the array was closer to the location that the feeder normally occupied than was the other end. This orientation potentially provided a stable reference point for the birds as to the ordinal positions of the flowers: the flower closest to the feeder location was always F1, the next was F2, and so on (Figure 1c). We had an array of 10 flowers, even though only four were ever rewarded, to control for the direction from which the birds approached the array.

Only one flower in the array was filled with 25% sucrose solution and the other nine flowers were empty. On each visit to the array, the hummingbird probed the artificial flowers until he discovered the rewarded position, fed, and flew away. A probe was defined as the bird lowering its bill into a flower's centrifuge tube (Figure 1b). The ordinal position of each probed flower was recorded. Following each visit, the positions of the individual flowers in the array were scrambled so that the bird could not learn to associate reward with small visual cues on the individual flowers, rather than their ordinal positions [30].

Training began with F1 rewarded. Once the bird had probed F1 first on four consecutive visits, the array was moved at least 60 cm from the location of the previous array so that the bird could not depend upon the absolute spatial location of the rewarded flower. The angle of the new array with respect to the feeder location was varied within the predetermined experimental arena, but one end of the array was always closer to the feeder location, to retain the reference point for the bird (Figure 1 c).

To move to the next phase of training (Training to flower F2), the bird needed to meet one of two criteria. If the bird visited F1 on his first visit to the moved array we considered that he had learned the ordinal position of the rewarded flower independent of its absolute spatial location, and the next phase of training could begin. Otherwise, the bird was required to search until he found the correct flower, and he had to visit F1 first on four consecutive visits. Then the whole array was moved again, to a new location, to test whether the bird had learned that F1 was rewarded independent of the spatial location. The training array was moved to a maximum of four different locations for each training flower before the training for the next ordinal location began. On reaching either criterion the bird was considered to have learned the ordinal position of the rewarded flower (Supplementary material F1).

This process was repeated for rewarded positions F2 and F3. When F4 was rewarded, training occurred as above, but with the addition of probe test trials, which were conducted on the completion of each training array. Once a bird had visited F4 first four consecutive times, the array was moved to a new location and the distance between the flowers within the array was varied as described below.

Test Protocol

Because during training flowers were always 20 cm apart in the array, the birds could have used distance from the edge of the array, rather than ordinal position, to locate the rewarded flower. To remove this possible confound, test trials were conducted in which the distances between the artificial flowers were varied.

A bird was presented with a test trial once he had reached one of the test criteria (four consecutive visits in which the first flower he probed was F4, or he probed F4 first on the first visit to a new array location after a previous test). Leaving the array in the same location as during training, the distances between the artificial flowers were varied: rather than 20 cm between each flower, the distance was either 10, 30, or 40 cm, with each distance appearing three times randomly throughout the array (Figure 1d). This resulted in the reinforced F4 occurring either nearer to F1 or farther away than it had in training. None of the flowers in the array were rewarded during test trials. The bird's first probe to the test array was recorded. Following this single visit, the array was moved as per the training protocol, and the next training trial presented (i.e. 10 flowers spaced at 20 cm intervals with F4 containing reward). Four test trials were conducted per bird, one after each of the F4-rewarded training arrays.

Analyses

Both training and test data from the combined visits of all birds to a particular location were analysed using one-sample and paired t-tests to determine the significance of percentage probes to each flower in all arrays for a given position. The effect that position of the flower had on the number of mistakes was analysed with a factorial repeated measures ANOVA. A Repeatability test was used to assess if the number of visits during each training phase was repeatable within a bird. A Friedman's ANOVA was used to compare the number of trials the birds took to learn the

four different ordinal positions. A chi-square test was used to determine whether during the four training trials birds were equally likely to visit the correct flower as to visit the adjacent flowers. We used Spearman's correlations to test whether the total number of trials or the number of trials when F4 was rewarded were correlated with the test performance of the hummingbirds. We used a binomial test to determine if the birds visited F4 more often than expected by chance at 0.10. All analyses were conducted using R version 3.3.2 [31].

Results

Training Trials

A total of 2094 probes made by nine males were recorded during the training phase of the experiment (F1 rewarded: 156 probes, F2: 482 probes, F3: 489 probes, F4: 967 probes). There was no consistency in the number of trials individual birds took to reach each flower's training criterion (Repeatability test with a Gaussian distribution, $r = 0.06$, 95% CI =0-0.38, $p = 0.40$). Data were analysed at the group level: for each rewarded position, the raw frequencies of probes to reach criterion for each flower by all birds were summed and transformed into percentages.

While the percentage of correct choices when the rewarded position was F1 was no different to that when the birds learnt that F4 was the rewarded position (Paired-samples t-test: $t_8 = 1.811$, $p = 0.108$), the birds took significantly fewer trials to learn the rewarded position F1 than they took to learn rewarded position F4 (Mean number of trials to reach criterion ± SE, F1: 17.33 ± 4.1; F2: 53.56 ± 11.43; F3: 54.33 ± 15.59; F4: 107.4 ± 16.59). The birds took significantly more trials to learn the different ordinal positions of the reward (Friedman's ANOVA, $X^2_3 = 19.81$, $p < 0.001$). Pairwise *Post hoc* tests with Bonferroni correction showed that the birds took significantly more trials to learn that F4 was rewarded than when F1 was

rewarded (difference = 24 where the critical difference was 14.45 with $\alpha = .05$). There was no difference in the number of trials taken to reach criterion between the other pairwise comparisons (e.g. F1 vs F2, F2 vs F3 and so on were all < 14.45).

For all rewarded positions, only the rewarded flower was probed significantly above the chance level of 10% (One-sample t-tests: F1 rewarded: $t_8 = 6.838$, $p < 0.001$; F2: $t_8 = 10.095$, $p < 0.001$; F3: $t_8 = 9.875$, $p < 0.001$; F4: $t_8 = 19.169$, $p < 0.001$; Figure 2A). When the rewarded position was F1, the birds probed all other non-rewarded flowers significantly below chance (all t-values $\leq$ -6, all $p < 0.05$). When the rewarded position was F2, the adjacent F1 and F3 were probed at chance (one-sample t-tests: F1: $t_8 = - 0.986$, $p = 0.353$; F3: $t_8 = - 0.016$, $p = 0.988$); all others were probed significantly below chance (all t-values $\leq$ -18, all $p < 0.05$). When the rewarded position was F3, the adjacent F2 and F4 were probed at chance (one-sample t-tests: F2: $t_8 = - 0.988$, $p = 0.352$; F4: $t_8 = -1.534$, $p = 0.164$). All other flowers were probed significantly below chance (all t-values $\leq$ - 4.4, all $p \leq 0.05$). Finally, when the rewarded position was F4, adjacent F3 was probed at chance (one-sample t-test: $t_8 = -0.378$, $p = 0.715$). All other flowers were probed significantly below chance (all t-values $\leq$ - 20, all $p \leq 0.05$).

In all cases, the birds chose the correct flower significantly more often than they chose the adjacent flowers ($X^2_3 = 8.52$, $p = 0.03$). When either F2, F3, or F4 were rewarded, which of these flowers was rewarded had no significant effect on the percentage of errors to either side of the correct flower (Factorial repeated measures ANOVA: $F_{2, 16} = 0.49$, $p = 0.61$). Specifically, birds were not more likely to make an error to the flower closest to the start of the array (near flower) or to the other side of the rewarded flower (far flower; $F_{1, 8} = 0.001$, $p = 0.97$) when either F2, F3 or F4 were rewarded (Figure 2B).

Test Trials

Each of the 9 birds completed 4 tests. They chose F4 a mean of 1.78 (±0.36) times. There was variation in individual performance, ranging from 0 to 4 choices. The performance during the test was not correlated with either the total number of trials the birds completed during the training ($r_s = 0.10$, $p = 0.79$) or with the number of trials birds took to reach the F4 criterion ($r_s = 0.05$, $p = 0.88$). Overall, F4 was chosen 16 times whereas chance performance would predict 3.6 times.

The birds probed F4 significantly more often than the chance level of 10% (one-sample t-tests: $t_8 = 3.782$, $p = 0.005$). They visited F1-3 and F5 at chance (one-sample t-tests: all t-values ≤ 1.131, all p-values ≥ 0.291), while all other flowers were visited significantly below chance (One-sample t-tests: all t-values ≤ -2.6, all $p \leq 0.032$; Figure 3A).

For arrays for which distance data were available (Supplementary material F2), F4 was located between 50 cm and 110 cm into the array, compared to the training distance for F4, which was always 60 cm. Therefore, the relative location of F4 in the test array compared to its location in the training array may have played a role in each bird's decision as to which flower to probe. Unfortunately, due to human error during data collection, the actual distances between flowers were recorded for only 22 of the 36 test arrays. Thus, we further analysed only the choices made by the hummingbirds during the tests for which we have distance data. Additionally, there was a 1/11 chance that the distance to F4 in training would be identical to the training distance of 60 cm. This redundancy of distances occurred in two of the test arrays for which distance was recorded, but may also have occurred during one or more of the test arrays for which distance data are missing.

252 During the tests for which we know the distance between flowers, ordinality (the 4th
253 flower) strongly influenced the choice made by those 6 birds (binomial test with an expected
254 proportion of 0.10 for F4: 9/22, $Z = 4.83$ $p < 0.001$). Exclusion of the two tests for which
255 distances were redundant (60 cm) made little difference to the significance of the results
256 (binomial test with an expected proportion of 0.10 for F4: 8/20, $Z = 4.47$ $p < 0.001$). Therefore,
257 they have been included in all later analyses.
258 Distance from the edge of the array did not strongly influence flower choice as neither
259 correct (F4) nor incorrect (other choices) were concentrated at or near the F4 training distance of
260 60 cm (Figure 3B). When a flower actually occurred at the 60 cm distance (6 times during the
261 tests) however, it was selected more frequently than chance (binomial test with an expected
262 proportion of 0.10 for the flower at 60 cm: 3/6, $Z = 3.26$, $p = 0.01$). Flowers occurring near or at
263 this distance (50, 60 or 70 cm) were probed more frequently than chance (binomial test with an
264 expected proportion of 0.10 for the flowers at 50, 60 and 70 cm: 6/22, $Z = 2.7$, $p = 0.01$). Birds
265 visited the 4th flower in the array in 41% of the tests, while the flower position at or closest to 60
266 cm was visited 27% of the tests. Errors were concentrated at the near end of the array with birds
267 visiting F1, F2 and F3 more often than expected by chance (binomial test with an expected
268 proportion of 0.10 for either F1, F2, F3: 10/13, $Z = 8.04$, $p < 0.01$).
269
270 **Discussion**
271 Rufous hummingbirds were tested for their ability to re-locate a rewarded artificial flower based
272 on its ordinal position in a linear array. During training, the birds probed only the rewarded
273 flower significantly above chance and did so consistently across four sequentially rewarded
274 positions: the birds were no more accurate at re-locating rewarded F1 than they were at re-

275 locating rewarded F4. Errors during training were concentrated around the flowers adjacent to
276 the rewarded flower, although at rewarded F4 the birds showed a bias toward erring on the
277 adjacent flower on the near side of the rewarded flower (i.e. F3). During testing, the distances
278 between the individual flowers in the array were altered so that distance information within the
279 training array was rendered ineffective. Above chance performance on the test arrays indicates
280 that the birds had encoded ordinal information during training and could apply it in the tests.
281 Additionally, during tests there was a clear directional bias to the birds' errors: most occurred on
282 the near side of the array, i.e. choices to flowers the birds had previously experienced as
283 rewarded. However, test choices were better explained by ordinal position than by distance from
284 the beginning of the array.

285 These data support the proposition that the birds used an object-indexing system rather
286 than a magnitude-based mechanism to determine the ordinal position of the rewarded flower.
287 This result is perhaps not surprising, as the analogue magnitude preverbal number system
288 appears to become salient only when animals process numerosities greater than four (e.g. [32]
289 but see [10]).

290 The distributions of errors that the birds made during training were not constant across
291 rewarded positions. When F1 was rewarded, the birds visited all non-rewarded flowers
292 significantly below chance. This could be because the birds learned to forage at the edge of the
293 array, rather than from the first ordinal position. When F2 and F3 were rewarded, in both cases
294 the two flowers adjacent to the rewarded flower were visited at chance (Figure 2A), indicating
295 that errors were mostly concentrated around the rewarded flower. This distribution of errors
296 could be the result of mistakes due to generalisation of the spatial location of the rewarded
297 flower: the bird learned that the reward was near the closest edge of the array. The distribution of

errors when F4 was rewarded however, was notable in that only F3, the adjacent flower on the near side of the array, was visited at chance: all other flowers, including adjacent F5, were probed significantly below chance. The tendency for the birds to make more errors towards the near edge of the array could be the result of a recency effect (i.e. a bias towards visiting a recently rewarded position). Rugani et al., [33], using a similar paradigm to investigate ordinality in chicks, controlled for past experience and observed a similar effect, attributing it to the birds using a 'working up' strategy to locate the correct ordinal position, similar to that observed in rats [17]. If the birds used one edge of the array as a reference point and mentally 'worked up' to find the correct ordinal position, they should have made more errors on the near side of array closest to the reference edge, in this case F1. This is exactly where the hummingbirds made their mistakes during the tests, closest to the F1 edge of the array. It is also how we trained the birds.

A working up strategy could relate to the way the hummingbirds perceived the array. Previous studies that used a similar paradigm to the present study were all conducted in the lab, allowing for a greater amount of control over the way in which the animals initially perceived the array, as the subjects' point of view could be controlled by designating a starting location for them. Subjects are more accurate when they can see the entire array at once, rather than encountering items in the array sequentially [e.g., 18]. Since the hummingbirds in this study were wild and took part in the experiment by choice, the way in which the birds visually perceived the array could not be controlled. Nonetheless, because the flowers were reasonably large, the training array was less than 2m in length, and birds could view the array from several metres above the ground, it can be assumed with relative certainty that the birds encountered the array visually as a whole and were thus operating similarly to laboratory subjects given a complete view of an array.

Overall, the distribution of errors during testing exhibited a directional bias that was a more extreme version of the effect demonstrated during training to F4. While during training the birds erred mostly on the near adjacent position, F3, during tests the birds additionally erred at F1 and F2, on a sizable proportion of visits. Unlike training at F4, the birds also visited F5, the other adjacent flower, at chance rather than below chance. Despite these differences, the birds' performance suggests that the birds were using the same ordinal strategy during testing as they were during training. If so, it follows that some aspect of the birds' ordinal strategy was confounded by the change in the test array. In other words, the 'working up' strategy posited to be the reason behind the directionally biased error effect in training was somehow exacerbated by the manipulation of inter-flower distances. It is possible however, that the birds were using both ordinal as well as distance information. When the distance information was made unreliable during the tests and even though birds did visit the fourth flower more often than expected by chance, when they made an error they made it to the flowers that were near the training distance.

A male rufous hummingbird may spend weeks or months in a territory, but the flowers from which he feeds will be far more ephemeral. Thus, a traplining hummingbird should be able to constantly adjust its trapline as some flowers bloom and others die. Using ordinality would allow this kind of flexibility. If each position in a hummingbird's trapline is assigned an ordinal value, the bird could follow this order and make adjustments as needed. If one location is no longer viable (e.g. the flower has senesced), then the bird could skip to the next ordinal position and strike the defunct flower from its trapline. Likewise, if a bird encountered a newly bloomed flower, it could adjust its trapline by inserting the flower in between adjacent ordinal positions.

As research into the numerical abilities of non-human animals has gained momentum over the past two decades, there is now broad consensus that animals perceive number and that

344 the ability for elementary numerical computation such as ordering units, is taxonomically
345 widespread, from arthropods to humans [34]. To our knowledge, our data represent the first
346 demonstration of numerical ordinality in a free-living wild vertebrate. It remains to be seen
347 whether numerical ordinality is governed by an object-indexing or an analogue magnitude
348 system of number, and to what extent the system used is a reflection of the birds' ecological role
349 as pollinators.
350
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Figure Legends

Figure 1. (a) Photograph of an array. (b) A rufous hummingbird probing an artificial flower. Photographs: Tom Oldridge. (c) Schematic of four possible training array positions. Flower positions F1-10 were determined based on the array's orientation towards the feeder. Distance between flowers is 20 cm. Note: during the experiment, the feeder was removed. One end of each array is always closer to the feeder location than the other, allowing the birds a reference point for determining which position was rewarded. F1 in each array is always at least 60 cm away from F1 of the previous array. (d) A training array (top) and an example test array (bottom). Circled flowers are the reinforced positions (no reward provided during test trials). Note: the distance from the first flower to the rewarded flower in the training array is 60 (20+20+20) while in the test array it is 110 (40+30+40). Figures not to scale.

Figure 2. A) The percentage of probes made by birds to each position, for each rewarded position during training trials (Mean +/- SEM). The dashed line represents chance at 10%. B) The percentage of errors made to flowers near (white bars) and far (grey bars) from the edge of the array when F2, F3, and F4 was rewarded (Mean +/- SEM). For example, when F2 was rewarded the "near" flower was F1 and the "far" flower was F3.

Figure 3. A) The percentage of probes by birds to each position of test arrays (Mean +/- SEM). The dashed line represents chance at 10%. B) Number of visits to flowers at different distances from the edge of the array. White bars represent visits to flowers that were not F4. Grey bars represent visits to F4 at different distances during the test. The red box represents the distance of F4 during training (at 60 cm).

Acknowledgements

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Figure1

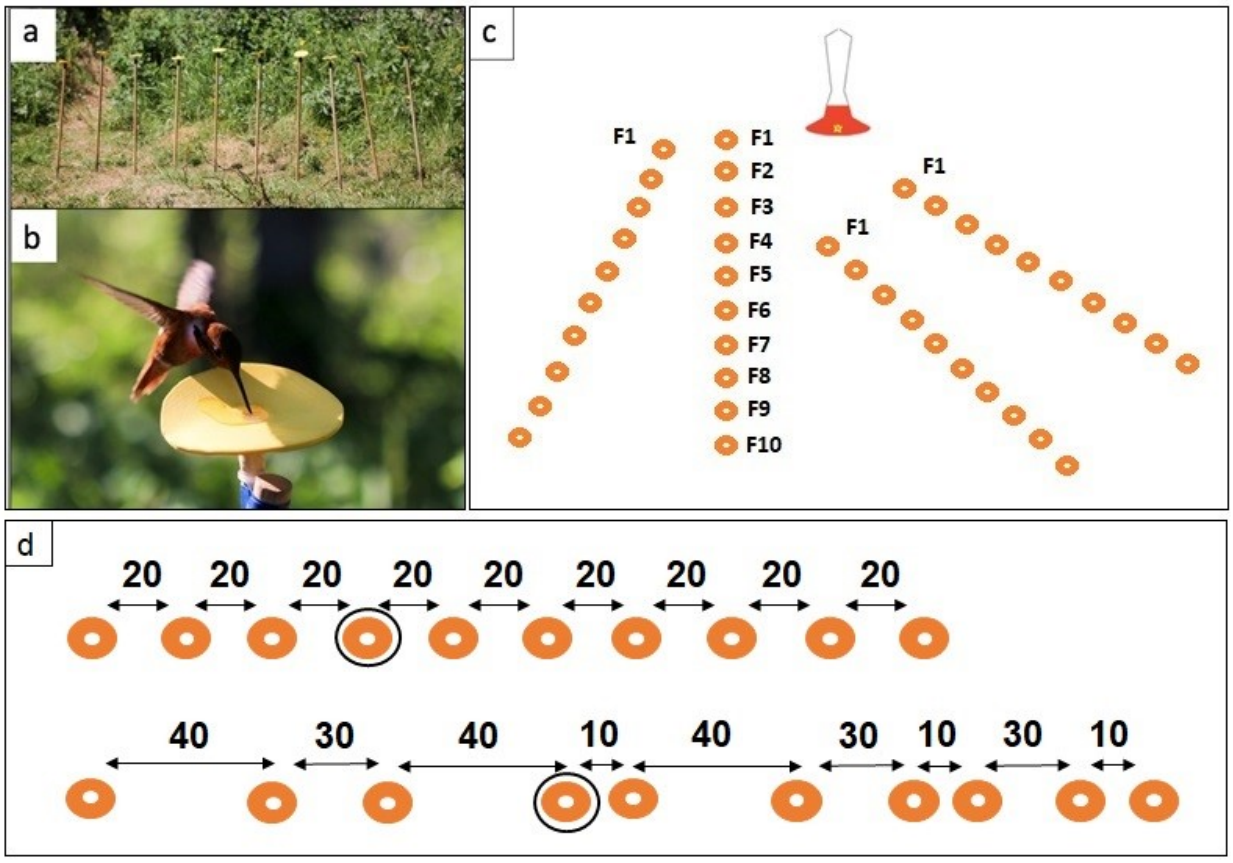


Figure 2

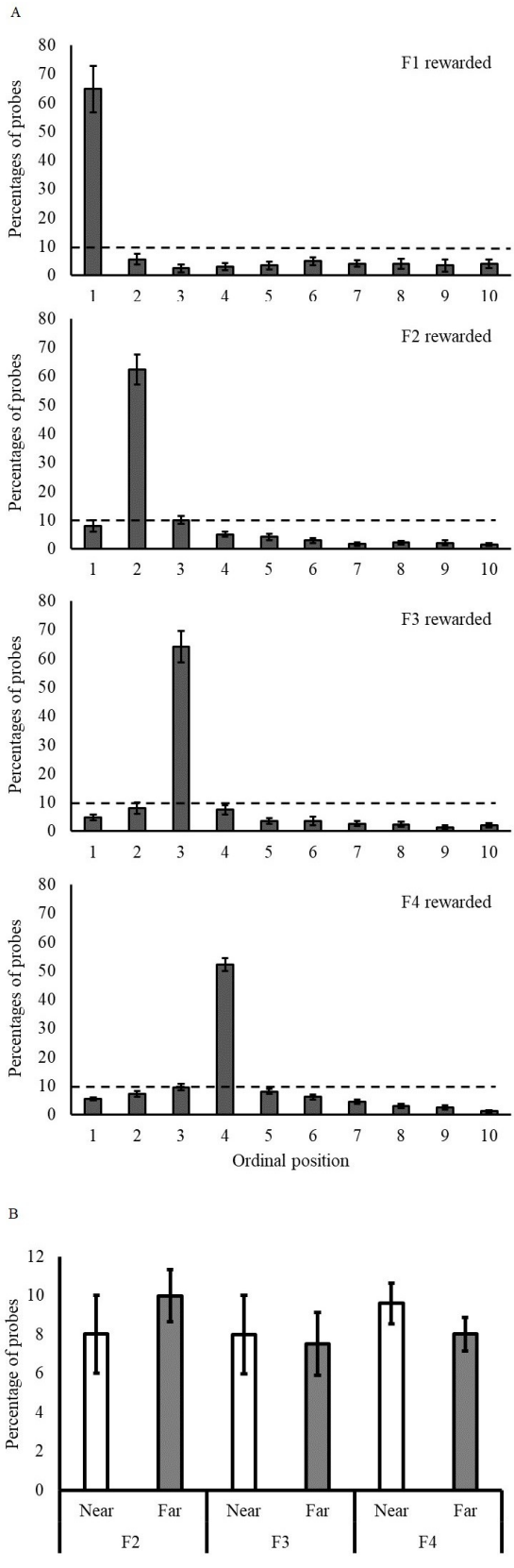
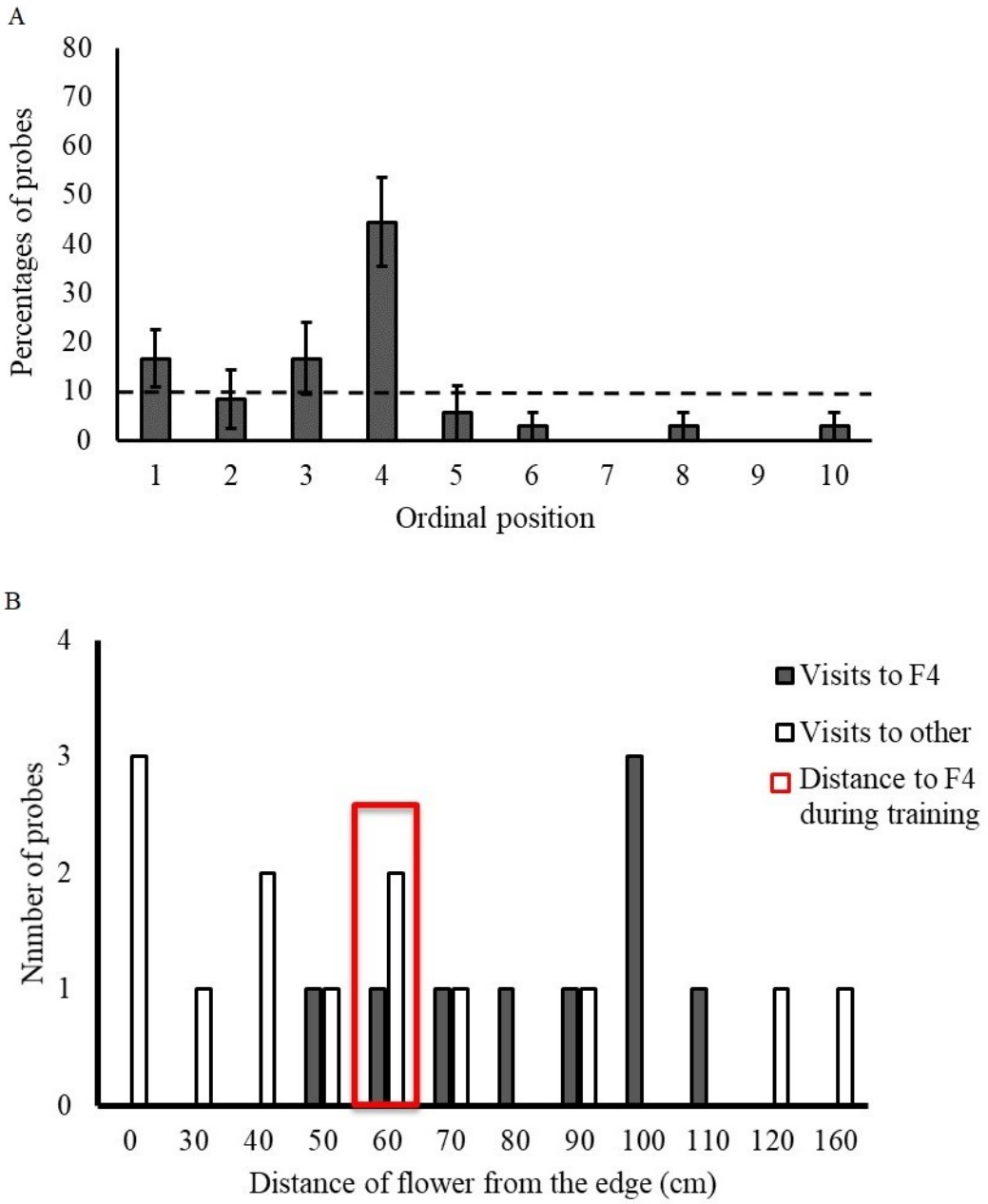
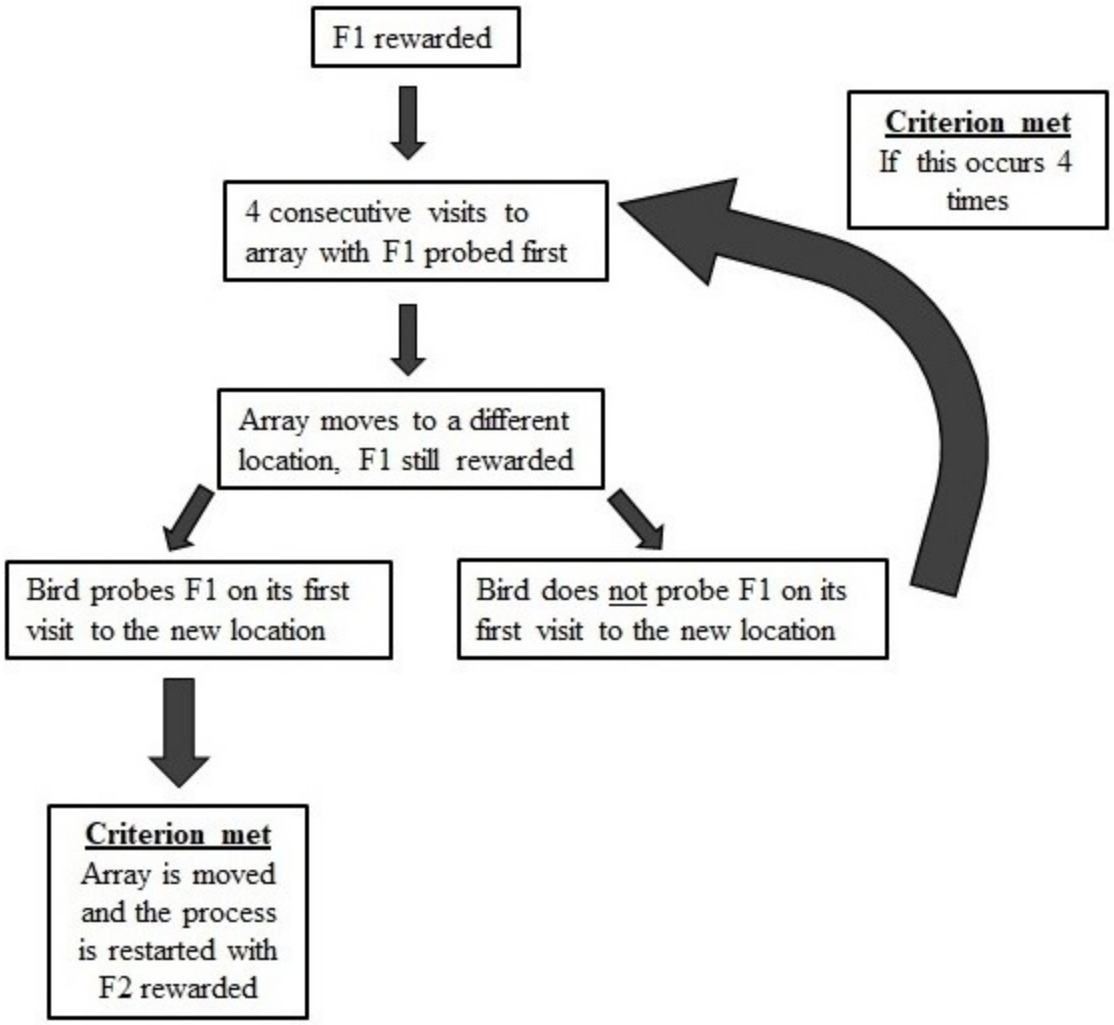

A
F1 rewarded
F2 rewarded
F3 rewarded
F4 rewarded
Percentages of probes
Ordinal position
B
Percentage of probes
Near
Far
F2
F3
F4

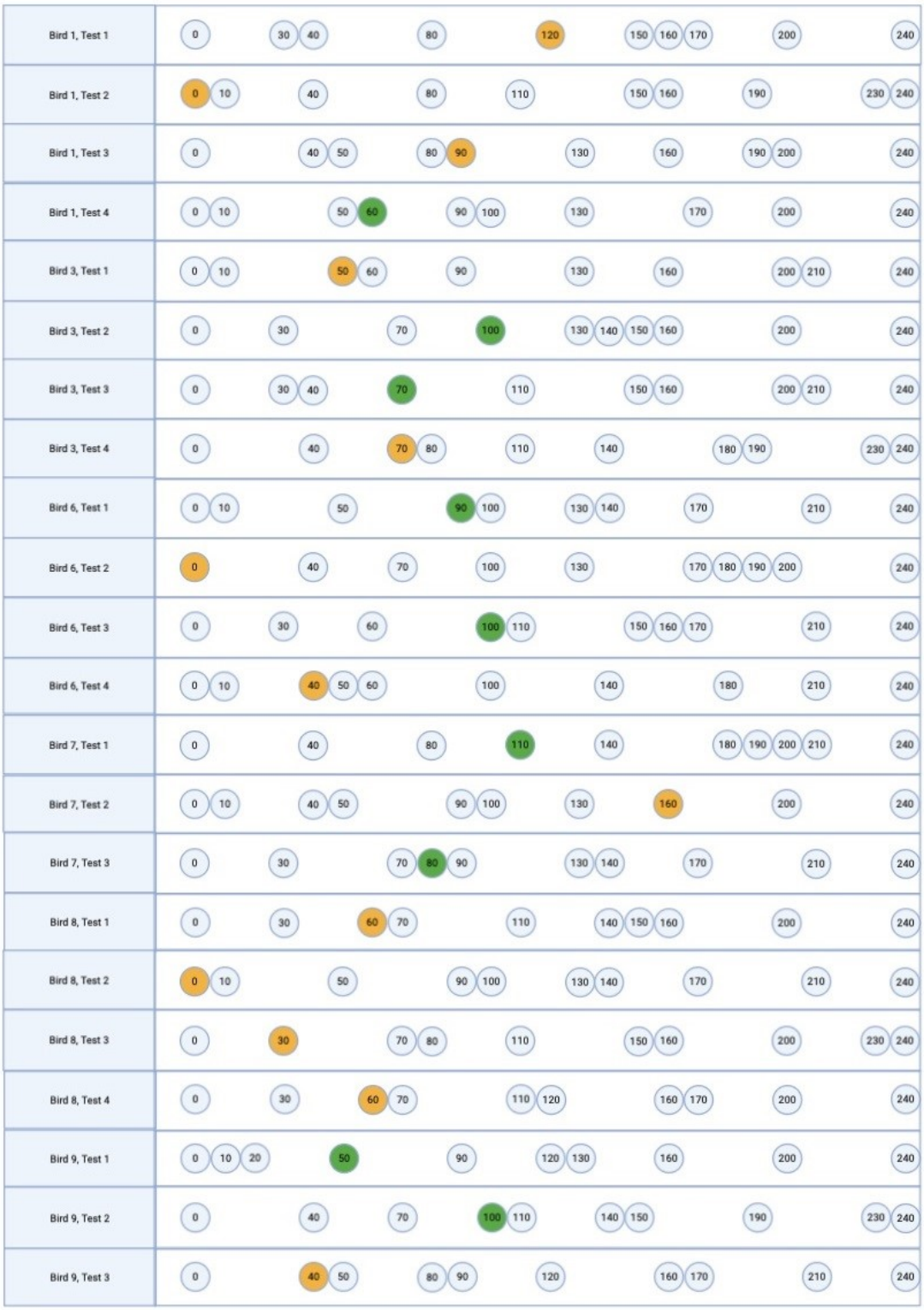
Figure 3


A
Percentages of probes
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
Ordinal position
B
Nnmber of probes
4
3
2
1
0
Visits to F4
Visits to other
Distance to F4 during training
0
30
40
50
60
70
80
90
100
110
120
160
Distance of flower from the edge (cm)

Supplementary material F1. Diagram of the training criteria. In order to move to the next phase of training, the bird needed to meet one of two criteria. Once a bird had visited four consecutive times the rewarded flower in first place the array was moved. If the bird visited the rewarded flower first at the new location we considered that bird had learned the ordinal position of the rewarded flower and the criterion was met. The bird was then trained to visit the next rewarded location. Alternatively, the bird was required to search until he found the correct flower and to visit the rewarded flower first for four consecutive visits. The training array was moved to a maximum of four different locations for each training flower before the training for the next ordinal location began. On reaching either criterion the bird was considered to have learned the ordinal position of the rewarded flower.



Supplementary material F2. Test arrays for which the distance between flowers are known (22 test for 6 birds). Circles represent flowers. The numbers inside each flowers are the distances from the edge of the array to that flower. The coloured flowers represent the bird's visit to that flower and were the green ones were probed 'correctly' (F4).



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